

ADAPTATIONS TO INTERTIDAL DEVELOPMENT: STUDIES
ON *NASSARIUS OBSOLETUS*¹

JAN A. PECHENIK²

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

Egg capsules of marine invertebrates are often described as "protective" (Carriker, 1955; Hunt, 1966; Mileikovskiy, 1971; Sverdrup, Johnson and Fleming, 1942), but the question of what the capsules protect against has rarely been addressed. The possibility that the egg capsules of the intertidal mud snail, *Nassarius obsoletus*, evolved as an adaptation to reproduction in the intertidal zone is considered in this study.

Although many marine gastropod and polychaete species deposit egg capsules or egg masses in the intertidal zone, the consequences of intertidal development to the developing young have not been examined. Houbrick (1973, p. 883) noted that the egg masses of *Cerithium variable* are "frequently exposed to sun and air during low tide," and "appear resistant to desiccation." Similarly, the jelly masses of the polychaete *Marphysa* are presumed to protect embryos from the sun at low tide (Aiyar, 1931), and the egg masses of *Littorina littoralis* (= *L. obtusata*) are said to protect developing embryos from desiccation (Fretter and Graham, 1962, pp. 389-390), but data in support of these suppositions are not given. Egg masses of the salt marsh pulmonate *Melampus bidentatus* can be desiccated for long periods of time, apparently without interference to embryonic development (Holle and Dineen, 1957). Whether the egg mass protects the embryos or whether the embryos themselves are especially tolerant of desiccation was not determined.

Spawning in the intertidal zone does not necessarily imply that developmental stages are resistant to intertidal stresses. Several authors have suggested that encapsulated invertebrate embryos are susceptible to desiccation (Spight, 1975; Kohn, 1961) and osmotic stress (Carriker, 1955; Gibbs, 1968). The walls of egg capsules from *Urosalpinx cinerea* are said to be freely permeable to a variety of organic and inorganic solutions, organic salts, and dyes (Carriker, 1955; Galtsoff, Prytherch and Engle, 1937).

Nassarius obsoletus deposits fertilized eggs in capsules affixed to firm substrates in the parental habitat (Dimon, 1905). The capsules, figured by Scheltema (1962), are approximately 1.5 mm high and contain 30 to several hundred eggs (Costello and Henley, 1971). The encapsulated embryos develop in the intertidal zone for approximately one week, after which time veliger larvae emerge from the capsules to continue their development in the plankton for at least several more weeks before metamorphosing to the benthos (Scheltema, 1962). While encapsulated, embryos are potentially exposed to intertidal stresses, the most obvious of which is desiccation. Kanwisher (1957) reports that relative humidities of 40% are com-

¹ Contribution number 3923 from the Woods Hole Oceanographic Institution.

² Present address: Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881.

monly observed in the intertidal zone. Successful development in the intertidal zone may require egg capsules which retard water loss at low tide, embryos capable of tolerating extensive dehydration, or preferential placement of the capsules in high-humidity situations. Alternatively, substantial pre-hatching mortality may occur. These possibilities were considered through determinations of desiccation tolerances of encapsulated *N. obsoletus* embryos, rates of water loss from *N. obsoletus* egg capsules relative to rates of water loss from capsules of the subtidal species *N. trivittatus*, and studies of the adult egg-laying behavior of *N. obsoletus*.

MATERIALS AND METHODS

Egg capsules of *Nassarius obsoletus* were removed from *Fucus* and eel grass collected at the Barnstable mudflats on Cape Cod, Massachusetts. Egg capsules of *N. trivittatus* were deposited in the laboratory by adults dredged from Buzzard's Bay, Massachusetts. Undamaged capsules of both species were sorted into two age groups before each experiment, based on the extent of anatomical differentiation of the enclosed embryos visible at a magnification of 25 \times . Capsules containing "early" embryos (no velum pigmentation or shell visible) were distinguished from those containing "advanced" embryos (distinct shell and easily discernible velum pigment). Only capsules completely full of eggs and containing embryos of a single age class were included in experiments.

Desiccation tolerance of encapsulated embryos was examined at two relative humidities, approximately 0% and 75% as determined with a Honeywell portable hygrometer. These relative humidities were achieved by covering the bottoms of glass jars with anhydrous CaSO₄ or a saturated solution of NaCl in distilled water (O'Brien, 1948), respectively. Age-sorted *N. obsoletus* capsules were spooned into perforated, plastic petri dishes, and most of the adhering water quickly blotted away. From 50 to 209 egg capsules were spooned into each dish. Large clumps of capsules were broken up into smaller groups, but no attempt was made to isolate each individual capsule. Each dish was suspended above desiccant in a jar which was then sealed. All experiments were conducted at room temperature, 22–23° C. The air in each jar was stirred by rocking the dish of capsules every fifteen minutes. At pre-determined intervals, one dish from each age class was removed from a jar, capped with a perforated top, and submerged in running sea water (approximately 30‰). One dish of egg capsules from each age class served as a control for its age group and was not subjected to desiccation, being placed in flowing sea water at the start of the experiment. Capsules suspended over distilled water for the entire exposure period served as additional controls; relative humidity within these jars was 100%, as determined with a Honeywell portable hygrometer. After treatment, the dishes of egg capsules were submerged in flowing sea water and examined periodically to assess survival. Tolerance of the stress was indicated by the eventual escape of veligers from the capsules. Capsules do not open spontaneously; a specialized hatching substance produced by the embryos is required for escape to occur (Pechenik, 1975).

Additional experiments were conducted to determine the effect of repeated exposures to low humidity air on pre-hatching mortality. Groups of capsules were

subjected to 75% relative humidity for either 0.5 hr or 2 hr each day, until hatching was completed after about 9 days.

The rates of water loss from intertidal *N. obsoletus* egg capsules were compared with rates of water loss from the morphologically similar, but primarily subtidally-deposited capsules of *N. trivittatus* (Scheltema and Scheltema, 1964). The magnitude of the differences found should reflect the degree to which *N. obsoletus* capsules are specifically adapted for their intertidal deposition. Ten to 12 min after the addition of CaSO₄ desiccant to the weighing chamber of a Cahn Electrobalance, a single egg capsule was blotted dry, dropped onto the weighing pan, and the weighing chamber was quickly resealed. Capsule weight was determined at 30 sec intervals for 15 min, or until the weight stopped changing between readings.

Data were obtained for 40 egg capsules, ten capsules for each of the two age groups for both species. The rate of weight loss was found to be constant for all capsules for the first 8.0 min after the start of each experiment. Hence, the rate of weight loss was computed from the weight change observed during this interval. Capsule weight at 1.5 min after the initiation of the experiment was taken as the "initial" weight. Since the rate at which water can be lost from a closed container is a function of exposed surface area, proportional to (weight)^{2/3}, the data were adjusted using the following expression before statistical comparisons were made between groups of capsules: adjusted rate = (mg lost/30 sec)/(initial capsule weight)^{2/3}. This manipulation substantially reduced variability in the data. Rates of weight loss discussed in the text are unadjusted rates, unless otherwise indicated.

The placement of *N. obsoletus* egg capsules with respect to substrate orientation was examined in the laboratory. Adults were collected from Quissett Harbor and Barnstable Harbor, Massachusetts, and held in aerated aquaria. Snails were fed every two to three days on chopped *Mercenaria mercenaria* tissue. A rectangular, plastic container with one curled edge on the upper surface was placed on the bottom of each tank, completely submerged in sea water, and the number of capsules deposited upon each surface of the container was determined on nine occasions over a 2-week period. All capsules were removed from the container after each observation, so that the extent of deposition on any surface was never limited by the area available.

The extent to which egg capsules are protected from exposure to low humidity air in the field was estimated by spraying exposed clumps of *Fucus* with blue enamel paint during low tide at Quissett Harbor and Eel Pond. The spray paint should have reached only those capsules exposed to the air, while capsules in more sheltered, high-humidity sections of the *Fucus* should have remained untouched by the paint. The *Fucus* clumps were then detached from their rocks and the numbers of blue, "speckled" (exhibiting from one to several small blue spots), and unpainted capsules on the algae were determined. The position of each capsule with respect to the basal 2 cm of algae was also recorded.

RESULTS

Desiccation tolerance of encapsulated embryos

Egg capsules of *N. obsoletus* did not afford substantial protection against desiccation. At 0% relative humidity, mortalities of at least 60% were sustained after

TABLE I

Mortality of encapsulated early-stage N. obsoletus embryos after single exposures to 75% relative humidity.

Treatment	Number of capsules	Exposure time (hr)	Mortality (%)
Sea water control	209	0	0.5
100% relative humidity control	111	5	0.0
75% relative humidity	156	1	0.0
75% relative humidity	123	2	3.3
75% relative humidity	126	2.5	1.6
75% relative humidity	151	3	2.6
75% relative humidity	141	3.5	12.5
75% relative humidity	167	4.5	10.2
75% relative humidity	169	5	15.7

a single exposure of less than one hour (Fig. 1). Substantial mortality of early-stage embryos resulted after only 15 minutes of exposure. Controls exhibited less than 5% failure to hatch. Even at 75% relative humidity, 12% of the capsules failed to release larvae after a single 3.5 hr exposure, while control mortalities were less than 0.5% (Table I). Clumping together of the egg capsules in the petri dishes probably accounts for the lack of increased mortality between 2 and 3 hours, since clumps would retain moisture longer than individual capsules. Although mortalities did not exceed 3.3% at 75% relative humidity for single exposures of less than 3.5 hr, daily exposures for considerably shorter periods, 0.5–2 hr, resulted in mortalities of approximately 15% (Table II).

Advanced-stage encapsulated embryos were significantly more tolerant of desiccation stress than were early-stage embryos (Fig. 1; $P < 0.05$, as tested by Chi-square). This indicates that age-related changes occur either in the water-retaining ability of the capsules or in the tolerance of the embryos themselves, as considered below.

Rates of water loss from egg capsules

There were no statistically significant differences in adjusted rates of water loss from capsules of different ages, for either *N. obsoletus* or *N. trivittatus*, as analyzed

TABLE II

Mortality of encapsulated N. obsoletus after daily exposures to 75% relative humidity. Capsules contained early-stage embryos at start of experiment.

Treatment	Number of capsules	Exposure time (hr)	Mortality (%)
Control	72	0	4.2
Control	131	0	3.0
100% relative humidity	122	1	4.1
100% relative humidity	50	2	0.0
100% relative humidity	143	2	0.0
75% relative humidity	63	0.5	17.5
75% relative humidity	73	2	12.3

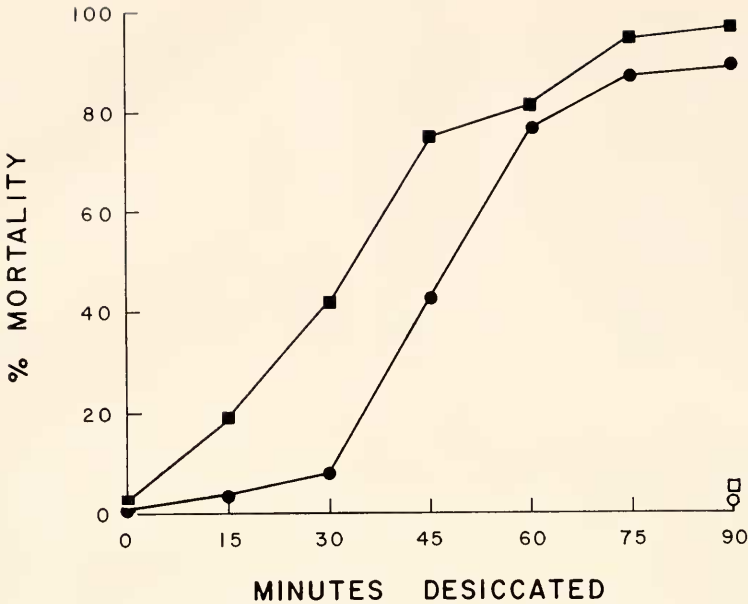


FIGURE 1. Desiccation tolerances of encapsulated embryos of *N. obsoletus*. Experiments were conducted over CaSO_4 desiccant. Circles represent data from capsules containing late-stage embryos ($N = 455$ capsules). Squares represent data from capsules containing early-stage embryos ($N = 293$ capsules). Open symbols indicate data from control capsules held at 100% relative humidity for the full 90 minutes.

by analysis of variance ($F_{N. trivittatus} = 1.94$; $F_{N. obsoletus} = 2.62$; $P > 0.1$; $N = 20$ capsules for each species). Since the water-retaining ability of the capsule itself does not change with age, age-related improvements in desiccation tolerance are attributable to a change in embryonic tolerance, possibly due to the development of the embryonic shell.

Egg capsules of both species lost weight at a constant rate for at least the first 8 minutes of observation. One-way analysis of variance revealed no statistically significant differences in the adjusted rates of water loss from egg capsules of the two different species ($F = 1.07$; $N = 20$ capsules for each species; $P > 0.1$). Thus, the water-retaining ability of the intertidally-placed *N. obsoletus* capsule is essentially identical to that of the subtidally-placed *N. trivittatus* capsule.

Rates of water loss (weight/unit time) from capsules similar in initial weight were essentially identical, regardless of capsule age or identity. Larger capsules lost weight more rapidly than smaller capsules, as expected. The relationship between the rate of weight loss (Y) and the weight of the capsule at 1.5 minutes after the start of the experiment (X) is given by the equation $Y = 0.027 + 0.015X$, as calculated by linear regression analysis (Fig. 2). The mean rate of weight loss from the 40 egg capsules was $0.044 \text{ mg}/30 \text{ sec} \pm 0.005$ (mean \pm s.d.). The differences in rates of water loss between egg capsules were due primarily to differences in the sizes of the capsules; the correlation coefficient (r) between rate of

weight loss (mg/30 sec) and "initial" egg capsule weight was 0.82 ($F = 80.85$; $N = 40$ experiments).

Placement of egg capsules in the laboratory

Capsules were not deposited randomly on the plastic containers (Table III). The differences in the numbers of capsules received by each surface of the container are significant at the 0.01 level, as tested by analysis of variance (d.f. = 11,96; $F = 4.7$). Statistical comparisons reveal two behavioral phenomena associated with capsule deposition. Low thigmokinesis (Fraenkel and Gunn, 1961) is revealed by particularly heavy deposition along edges, under the curled edge, or underneath the platform, regions maximizing the amount of contact stimulation of the foot of the depositing female. There is also an orientation component, specifically a preference for depositing while hanging. The fewest capsules were attached to the bottom and outside top surfaces of the container. The correlation coefficient (r) between the number of capsules deposited and available surface area on the different surfaces of the container was 0.36, indicating that placement preferences were not related to the amount of surface area available.

Capsules were never deposited above the water line in laboratory aquaria, suggesting that capsule deposition in the field occurs only when the substrate is submerged.

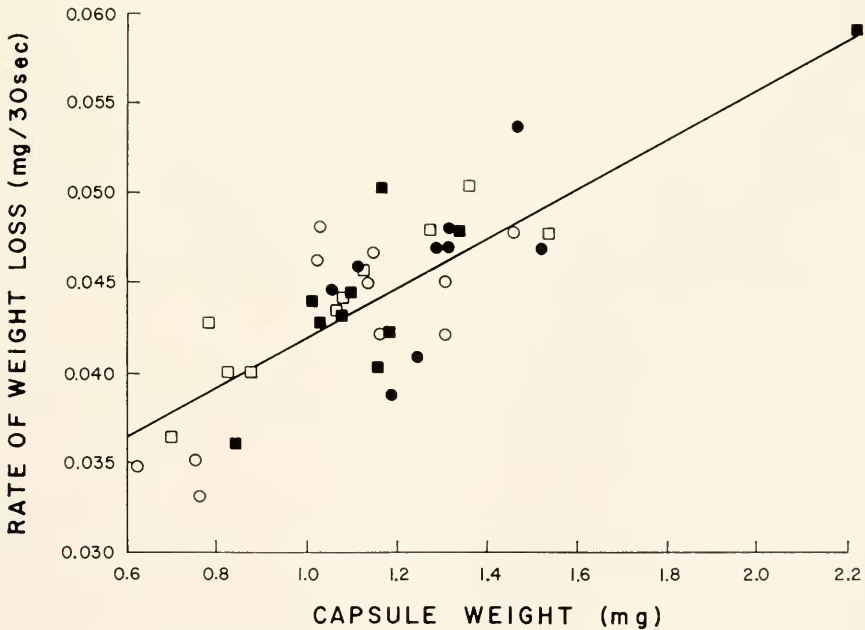


FIGURE 2. Rate of weight loss for desiccating egg capsules of *N. obsolctus* (squares) and *N. trivittatus* (circles) as a function of "initial" capsule weight. Open symbols represent data obtained from capsules containing early-stage embryos, while solid symbols represent data obtained from capsules containing advanced-stage embryos.

TABLE III

Distribution of N. obsoletus egg capsules deposited on plastic containers in the laboratory.

	Quissett Harbor adults	Barnstable Harbor adults
Total capsules deposited	855	501*
Percentage of capsules deposited on:		
Bottom	1.6	2.0
Back	18.5	4.7
Sides	9.8	6.1
Top (inside)	16.0	17.2
Top (outside)	1.2	0.0
Edges (inside)	21.9	64.0
Edges (outside)	11.0	5.0
Under curled edge	20.0	1.0

* This container was improperly anchored. An additional 101 capsules were deposited on the underside of the container.

Placement of capsules in the field

Due to the low thigmokinetic component of the adult egg-laying behavior, one expects to find more capsules deposited near the holdfast of *Fucus* than upon other portions of the algae, owing to the closeness of individual strands in the holdfast area relative to other sections of the algae when submerged. One would also expect most of the capsules to be deposited on the undersides of the strands, due to the apparent preference for hanging while depositing.

Capsules on *Fucus* collected at Quissett Harbor were located primarily in the region of the holdfast, as predicted (Table IV). Although this did not hold true for Eel Pond *Fucus* on a strictly numerical basis, many more capsules were deposited in the holdfast region than elsewhere on the algae when the relative surface areas (estimated by dry weight) available for deposition of capsules were considered. One hundred capsules/gram algae were found in the region of the holdfast and 11.6 capsules/gram algae were found elsewhere, based on examination of four plants, and counts of 68 and 235 capsules in the basal and distal regions of the algae, respectively.

The pattern of paint on egg capsules was similar for tufts of *Fucus* sprayed at both locations at low tide, so that only the results from Quissett Harbor are presented here (Table IV). Most of the capsules were at least partially protected from exposure to low humidity air, fewer than 8% of the capsules being entirely

TABLE IV

Distribution and color of 583 N. obsoletus egg capsules recovered from Fucus spray-painted at low tide at Quissett Harbor, Massachusetts.

	Holdfast	Nonholdfast
Deposited in zone	69.0%	31.0%
Blue capsules	7.7%	4.4%
Unpainted capsules	8.0%	13.3%
Speckled capsules	84.3%	82.3%

exposed at low tide. Speckled capsules, which generally exhibited only one or two small spots of paint, can probably be considered as being protected.

The dearth of firm substrate available to the large *N. obsoletus* population on the Barnstable mudflats results in the attachment of capsules to all available surfaces; suitable macro-algae are literally covered with capsules. Since much of this material is completely exposed to air at low tide, pre-hatching mortality here may be high. Dried and shrunken *N. obsoletus* egg capsules are frequently encountered. Of 664 egg capsules collected at the end of a low tide at Barnstable early in August and held in flowing sea water in the laboratory, 28% failed to release veligers. As most of these capsules contained early-stage embryos when collected and because repeated exposure to low humidity air increases mortality significantly, as demonstrated above, 28% is probably a minimum estimate of the total pre-hatching mortality that would have occurred had the embryos been allowed to complete their development in the field.

DISCUSSION

Caution must be used in relating experimental data on embryonic desiccation tolerances and rates of water loss from egg capsules to actual events in the field. Relative humidities of 0% are unlikely to occur normally, although relative humidities of 40% are not uncommon in the intertidal zone (Kanwisher, 1957). Experiments conducted at 0% relative humidity demonstrate two important points, however. First, encapsulated embryos of *N. obsoletus* are more susceptible to desiccation stress than are the embryos of *Melampus bidentatus* (Holle and Dineen, 1957). The apparently lower susceptibility of *M. bidentatus* embryos to desiccation is surprising; although the egg masses are deposited high in the intertidal zone, an accumulation of detritus around them probably prevents their desiccation (Russell-Hunter, Apley and Hunter, 1972). Secondly, the egg capsules of *N. obsoletus* are no more effective in retaining water than are capsules of the subtidal *N. trivittatus*. Bayne (1968) obtained similar results with the egg capsules of the intertidal gastropod *Nucella lapillus*. Rates of water loss [$\text{mg}/(\text{min} \cdot \text{unit surface area})$] from egg capsules of this species were nearly identical with those from the normally submerged spawn of both the opisthobranch *Aplysia punctata* and the basomatophoran *Lymnea stagnalis*.

It is not possible to predict the actual extent of pre-hatching mortality from the experimental data presented here. The impact of desiccation in the field will vary with humidity, temperature, duration and degree of exposure, wind velocity, and the thickness of any boundary layer that may be present above the capsules. The important points are that substantial pre-hatching mortality of *N. obsoletus* occurs in the laboratory after even a single, short exposure to 75% relative humidity, and that daily exposure to desiccation results in significantly greater mortality than that observed after a single exposure. Substrates literally encrusted with *N. obsoletus* egg capsules are often found completely out of the water at low tide on the Barnstable mudflats. In such cases, pre-hatching mortality must be high, since the egg capsules are not effective in preventing water loss and the embryos are not particularly tolerant of dehydration. Spight (1975) reported pre-hatching mortalities of

approximately 40% for intertidally-deposited *Thais lamellosa* egg capsules; desiccation was a major cause of this mortality.

There is, therefore, no evidence that gastropod egg capsules are specifically adapted for placement in the intertidal zone, and it seems unlikely that egg capsules evolved as adaptations to intertidal stresses.

Protection of the encapsulated embryos of *N. obsoletus* seems dependent upon adult behavior. Because capsules are placed on the undersides of *Fucus*, they are kept moist by the blanketing effect of the seaweed above them. Detailed experimental work on egg capsule placement preferences is lacking for most marine invertebrates (Meadows and Campbell, 1972), but the protection of early developmental stages through adult spawning behavior appears widespread in marine gastropods. Kudinsky (1972) claims that eggs of the prosobranch gastropod *Testudinalia tessellata* are laid preferentially in situations where they are spared direct exposure to sunlight. The egg capsules of *Conus spp.* (Kohn, 1961), *Cypraca spp.* (Crovo, 1971), shallow-water columbellid gastropods (Bandel, 1973), *Urosalpinx cinerea* (Carriker, 1955), and *Bembicium auratum* (Anderson, 1962) are deposited on the undersides of rocks, presumably to prevent desiccation (Anderson, 1962; Kohn, 1961), and the archaeogastropod *Neritina virginea* is said to deposit its capsules preferentially in crevices (Andrews, 1935).

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SUMMARY

1. The extent to which reproduction of the intertidal mud snail, *Nassarius obsoletus*, is adapted to the intertidal environment was examined in an attempt to understand the adaptive significance of egg capsules in the life history.

2. Contrary to expectation, laboratory studies on desiccation tolerance of encapsulated embryos and rates of water loss from egg capsules failed to reveal any adaptation to intertidal development. Fifteen minutes of desiccation over CaSO_4 caused as much as 20% mortality of *N. obsoletus* embryos, and daily 0.5 hr exposures to 75% relative humidity killed 17.5% of the embryos. Egg capsules of *N. obsoletus* and those of the subtidal *N. trivittatus* lost water at essentially equal rates.

3. Protection of the developing embryos seems dependent upon adult behavior. Adults tend to deposit egg capsules into microenvironments where the embryos are probably spared exposure to desiccation stress at low tide. Fewer than 8% of the capsules examined at Quissett Harbor, Massachusetts, were fully exposed to desiccation.

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